1988

The importance of diel periodicity and selectivity in the feeding behavior of the predatory copepod Mesocyclops edax /

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THE IMPORTANCE OF DIEL PERIODICITY AND SELECTIVITY IN THE FEEDING BEHAVIOR OF THE PREDATORY COPEPOD *MESOCYCLOPS EDAX*

BY

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A Thesis

Presented to the Graduate Committee

of Lehigh University

in Candidacy for the Degree of

Master of Science

in

Biology

Lehigh University

1987

CERTIFICATION OF APPROVAL

This thesis is accepted and approved in partial fulfillment of the requirements for the degree of Master of Science.

December 16, 1987

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ACKNOWLEDGEMENTS

I would like to acknowledge Craig E. Williamson and Mark E. Stoeckel for their participation in data collection and analysis. The use of Dr. Williamson's data to estimate ingestion rates from laboratory enclosure experiments was especially valuable to this study. I would also like to thank Dr. Sidney Herman and Dr. Bruce Hargreaves for their input and support throughout this project.

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ABSTRACT

Studies that attempt to estimate predation rates or determine selectivity from short term laboratory experiments (< 24 hours) may be over- or underestimating the results of the experiment unless the daily changes in the feeding behavior of the organism are considered in the experimental design.

Diel periodicity in the feeding behavior of the predatory copepod, Mesocyclops edax is reported for two 24 hour sampling dates on 9 July and 5 August, 1986. An increase in feeding activity occurred at 1130 and 2030 in July and 2030 in August. The increase in feeding activity at these times could not be explained by an increase in prey density, changes in predator-prey overlap, or prey vulnerability. However, low light levels at 1130 in July may have stimulated the peak in the feeding behavior of M. edax at this time.

Vanderploeg and Scavia's (1979) E* selectivity index was used to examine selectivity for three major food groups (rotifers, cladocerans, and copepods). Between the July and August dates selectivity remained generally the same with rotifers selected over cladocerans and cladocerans selected over copepods. However, the selectivity for the major food groups shifted somewhat over 24 hours. The daily shifts may be related to changes in predator-prey overlap while the seasonal shifts are attributed to changes in species composition between the two months. The abundance of rotifers in the diet for both months suggests the impact of predation on rotifers will be substantially higher than on the cladocerans or the copepods.

Daily changes in the feeding behavior and changes in the selectivity of M. edax illustrate the importance in timing of experimental designs in feeding behavior.

experiments. Without consideration of daily rhythms, short term experiments may give erroneous results

Ingestion rate estimates were obtained using two different techniques: 24 hour enclosure experiments using natural prey assemblages and gut content analysis from preserved animals collected over 24 hours in the field. Comparison of the results indicated that the two techniques were statistically indistinguishable.

INTRODUCTION

One goal in studying the feeding behavior of carnivorous zooplankton is to estimate the impact of predation on the zooplankton community. Laboratory studies on predation rate estimates are useful only if the factors influencing these rates are considered in the design of the experiment. Most authors consider temperature, light, pH, hunger level, and prey density, but neglect the possibility of a diel periodicity in feeding behavior or the effect of vertical migration. Often feeding rates of zooplankton are expressed on a daily basis calculated from short term experiments which could cause errors especially if these rates are used as the basis for further calculations of energy transformation in zooplankton populations.

Mesocyclops edax, a predatory cyclopoid copepod with widespread distribution in the United States and Southern Canada, has been widely studied in both field and laboratory experiments. Many of these studies have focused on the different aspects of its feeding behavior including: feeding mechanisms (Fryer, 1957), dietary differences in different life stages (Brandl & Fernando, 1986), foraging behavior (Williamson, 1981), prey selection (Brandl & Fernando, 1978; Williamson, 1981, Williamson & Magnien, 1982,), and the impact of predation on prey populations (Confer, 1971, Brandl & Fernando 1978, 1979, 1981). However, none of the studies has addressed the question of diel periodicity in the feeding behavior along with the changes in migrational patterns demonstrated by Mesocyclops edax.

Diel vertical migration by zooplankton, such as that demonstrated by Mesocyclops edax (Woodmansee & Grantham, 1961, Williamson & Magnien, 1982), is a widespread phenomenon that must be considered in feeding experiments. The differences in the extent

of vertical migration patterns of predators and prey can place the predators in prey environments that differ in prey number and prey type over a 24 hour period. Not only can prey number and prey type change, but the selection for certain prey items may also change over this time. Although the changing environment of the migrators may cause them to exhibit changes in their feeding times as well as their feeding preferences, the feeding activities of zooplankton during their migrations are not well known and evidence is often conflicting (Haney & Hall, 1975; Lampert & Taylor, 1985).

Studies of changes in the feeding rhythms of marine zooplankton have demonstrated that feeding activity does change over the day (Wimpenny, 1938; Gauld, 1951; Bainbridge, 1958; Petipa, 1964; Mackas & Bohrer, 1976). Diel changes in the feeding rates of freshwater zooplankton have also been reported in the field (Haney & Hall, 1975; Duval & Geen, 1976; Haney, 1985) and in the laboratory (Starkweather, 1983). However, these studies have been done primarily on Daphnia and other herbivores and not on predatory copepods alone (but see Duval & Geen, 1976).

Feeding studies must also consider the selective nature (if any) of the predator. The changing environment of the prey may cause changes in what is eaten at different times of the day. Bowers & Vanderploeg (1982) looked at the diel migrations of Mysis relicta in Lake Michigan and found that changes in overlap between predator and prey caused changes in ingestion with the predator feeding on diaptomid copepods at night and cladocerans by day.

Due to the highly selective nature of Mesocyclops edax (Brandl & Fernando, 1978; Williamson, 1980, 1983; Williamson & Magnien, 1982), their predation can have a dramatic effect on prey community structure. If Mesocyclops feeds primarily on the

smaller component of the zooplankton community copepod predation will have a greater impact on organisms such as the rotifers. Not only will the predators remove large numbers of prey from the aquatic ecosystem, but their selective predation could result in evolutionary changes in the morphology and behavior of the most heavily preyed upon species.

A variety of selectivity indices have been formulated to describe prey preferences of predators (see Lechowicz, 1982 for review). A widely accepted index in aquatic ecosystems is Vanderploeg and Scavia's (1979) selectivity index (E*). However, E* does not consider spatial or temporal overlap between predator and prey but assumes a homogeneous environment, I did, however, use this index with corrections for the changes in predato-prey overlap

My goals in this study were to examine the feeding behavior of Mesocyclops edax by means of gut contents analysis over a 24-hour period in July and again in August to determine 1) whether a diel periodicity in feeding occurred, and 2) the selective nature of Mesocyclops.

METHODS

The study area, Hellertown Reservoir, is a small (less than 1 hectare surface area) mesotrophic lake with a maximum depth of approximately 11 meters, located in Hellertown, Northampton County, PA (,). Weekly plankton samples were taken from May 15 - August 26, 1986 and followed this regime at 12:00h and 24:00h. To examine the migrational patterns of all zooplankton species, replicate samples from one site were taken at odd meters (1-9) using a transparent 8.2 l Van Dorn bottle. 7.9 l of the sample were filtered through a rotifer cone (Likens & Gilbert, 1970) fitted with 48 µm mesh, narcotized with carbonated water and preserved in cold sucrose formalin (40 g sucrose/l formalin, Prepas, 1978). Densities were estimated by counting 2-3 1 ml samples of large crustaceans (crustaceans, copepods) in a Bogorov chamber under a dissecting microscope and at least 100 rotifers and nauplii in 1 ml samples using a Sedgewick-rafter chamber under a compound microscope. Light and temperature readings were measured at every meter (0-10) and Secchi depths were recorded for each sampling date. Replicate vertical tow samples from 10 m were taken using a 60 cm diameter Wisconsin net fitted with a 202 µm net and the zooplankton preserved in the manner above. The sampling procedure was carried out by Craig E. Williamson, Mark E. Stoeckel, and myself as part of a larger scale project.

Two 24 hour studies were performed 9 July and 5 August, 1986. The sampling regime used was the same as the one for the weekly sampling above except that the samples were taken every 3 hours starting with 0530 and ending at 0230 (eight sampling times).

For the gut content analysis only adult females carrying eggs were used. Females were chosen because they are more voracious feeders. The use of nongravid females carrying

eggs insured the physiological state of the animals would be more uniform. Only females from the vertical tow samples were used because it would have been impossible to determine where the copepods were feeding prior to collection. Twenty copepods were examined at each time period to equal a total of 160 guts for each month.

The metasomal gut tubes were dissected out of the animals on a slide containing a small drop of water. Once the gut tube was isolated, a small drop of commercial bleach was added to the gut in order to dissolve inorganic particles and make rotifer trophi identifications possible (Williamson, 1984). The contents were observed under a 400X compound microscope and scored as rotifers, cladocerans, or copepod remains. Only the rotifer trophi were identified to species (except Polyarthra vulgaris and P. remata were counted as one species and all Keratella species were counted as one species). Cladoceran and copepod remains were scored as one prey item unless evidence of more than one appendage was found in a single gut. Of the 320 guts examined, 25 unknowns, and two algal genera (Peridinium and Scenedesmus) which were only seen several times were not added into the selectivity analysis.

Figure 2 which represents the mean number of prey per gut was calculated by taking the number of prey eaten during one time period and dividing it by the total number of predators examined during each time period (20).

To account for overlap of predator and prey the following formula was used:

$$\text{overlap value} = (\Sigma n_{iz} N_z) / (\Sigma n_{iz} \Sigma N_z)$$

where n_{iz} = density of prey species i at depth z (n_i = average density of prey species i in the water column. i = 1 to 19)

N_z = predator density at depth z (N=average predator density in reservoir

z=1-9 meters)

Weighted density (WD)was obtained by multiplying actual average density in the water column times the overlap value.

Two changes in Vanderploeg and Scavia's (1979) E* value were made to account for two problems: one change was made to account for the changes in overlap between predator and prey; that is, I used the weighted density in the formula instead of the actual density. The second change made was to account for gut passage time estimated at 3 hours (Williamson, 1984). Williamson found that after three hours, 20 % of the rotifer Brachionus calyciflorus trophi still remained in the gut. To account for this I used 80% of the weighted density from the time period being studied and added it to 20% of the prior time period' s weighted density to get a density which was more representative of gut passage time.

Laboratory experiments to obtain estimates of the clearance rates were carried out in the laboratory by Craig E. Williamson on 9 July and 5 August, 1986. The details of the procedure are found elsewhere (Williamson et al. in prep.) but consisted of collecting whole water discrete depth samples at 1, 3, 5, and 7 m and mixing them together to form a homogeneous mixture. This mixture was then divided into 12 individual 1 liter bottles and twenty adult female M. edax were added to half of the bottles. The other half of the bottles acted as controls and received no additional copepods. The copepods added to the experimental bottles were collected from the field samples immediately before the experiment began. A moving plankton wheel carrying the twelve 1 liter bottles was incubated for 24 hours at 20º C (the temperature of the zooplankton mixture obtained

from the discrete depth samples). The clearance rates were estimated from the standard exponential equations (Gauld, 1951; Dodson, 1975) and regression analysis (Lehman, 1980; Landry & Hassett, 1982; see also Williamson et al. in prep.).

The Chi Square Goodness of Fit test was used for all statistical tests except for the nonparametric Wilcoxon 's Signed-Ranks Test for Two Groups, Arranged as Paired Observations which was used to compare ingestion rate estimates from gut content analysis and ingestion rate estimates from enclosure experiments. All statistical tests used raw count data for the Chi-Square tests and tested intrinsic hypotheses except for the test for significant changes in E* and the test on the two techniques used in the nonparametric Wilcoxon Signed-Ranks Test (Sokal& Rohlf, 1981) The test for changes in the E* values used the occurrence of a prey item as the observed and the weighted density found in the water column at that time as the expected

There were limitations to the comparison of ingestion rates. Ingestion rates from Williamson's enclosure experiments were compared to ingestion rates from gut content analyses. Ingestion rates for gut contents were taken from the remains found in the gut Indentifcation for all rotifers to species was possible except Polyarthra in which there were three species represented. Only one of these was identified to species. The other two species were lumped together and counted as one species (P. remata and P. vulgaris) In the case of the cladocerans and copepods identification between species was not possible because the remains often consisted of feeding appendages or an abdominal claw in the cladocerans which were very hard to distinguish without other identifying parts and in the case of the copepods, only parts of the carapace or antennae were found and sometimes a caudal section but often it was torn so that identification to species was not possible

Therefore the data for the cladocerans was lumped and averaged as one species and the same was done for the copepods Due to these limitations and the fact that not all available prey species were eaten, only 8 species in July and 6 species in August were compared

RESULTS

Results of the gut content analyses indicate different numbers of prey items were eaten by Mesocyclops edax throughout the 24 -h sampling on 9 July and 5 August, 1986 in Hellertown Reservoir (Figure 1). The greatest number of prey eaten were at 1130 and 2030 in July and 2030 in August and the difference in the numbers eaten over 24 hours is significant for each month at the P=0.001 level. However, not all guts were full at all time periods (Figure 2). The highest percentages of full guts were found at 0530 and 2030 in July and 2030 in August and the highest percentages of empty guts were found at 8.30, 2330, and 0230 in July and 0830, 1430, and 1730 in August. However, none of these differences in gut fullness were significant (P>0.05) over 24 hours. Figure 3 represents the mean number of prey per predator gut and shows that an increase in number of prey per predator gut is seen at 1130 and 2030 in July and 2030 in August. The number of prey items in the gut over time was significant (P=0.5) suggesting that further investigation into the diel periodicity in feeding is warranted. Other factors that could cause an increase in feeding activity must be considered. prey availability in terms of numbers, overlap of predator and prey in time and space, and prey vulnerability.

Increases in prey density cause an increase in ingestion rates in Mesocyclops edax (Confer, 1971). An increase in the ambient prey density at the times of peak feeding could be responsible for the significant increase in the prey items ingested. Total densities for all zooplankton species, including the cannibalistic predator, show significant differences (P=0.0001) in abundance over time in both months (Figure 4). However, there are no peaks in in density at 1130 and 2030 in July and 2030 in August which could account for the increase in feeding at these times.

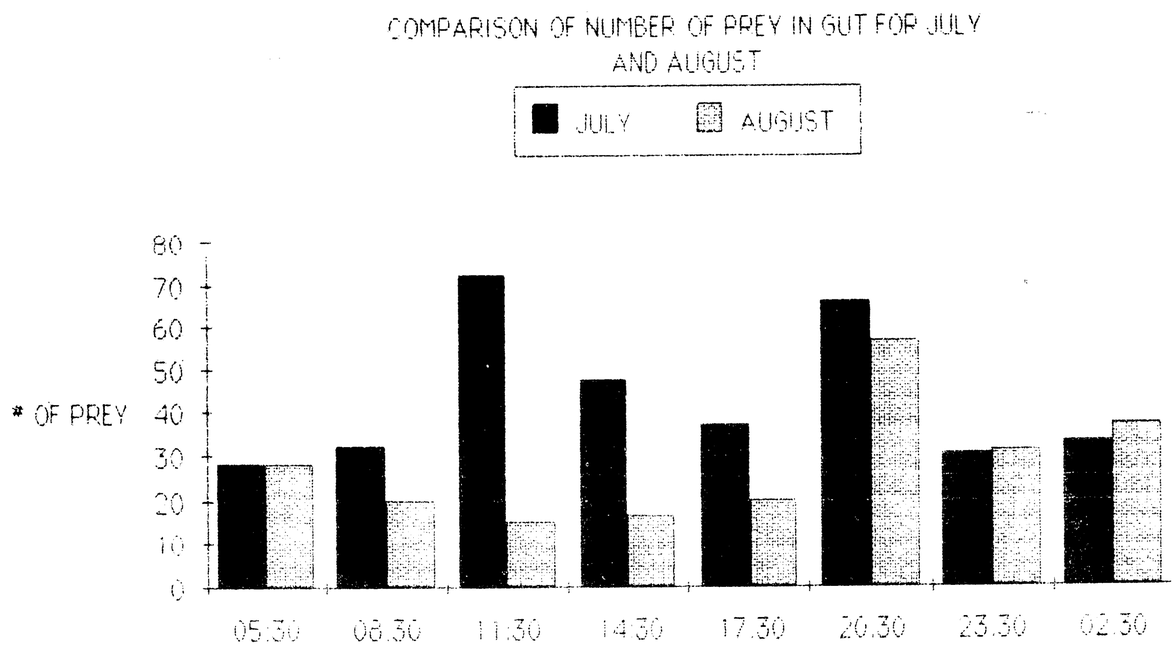


Figure 1 Total number of prey items found in 20 guts during each sampling period in July and August. Numbers include rotifers, cladocerans, and copepod prey items combined.

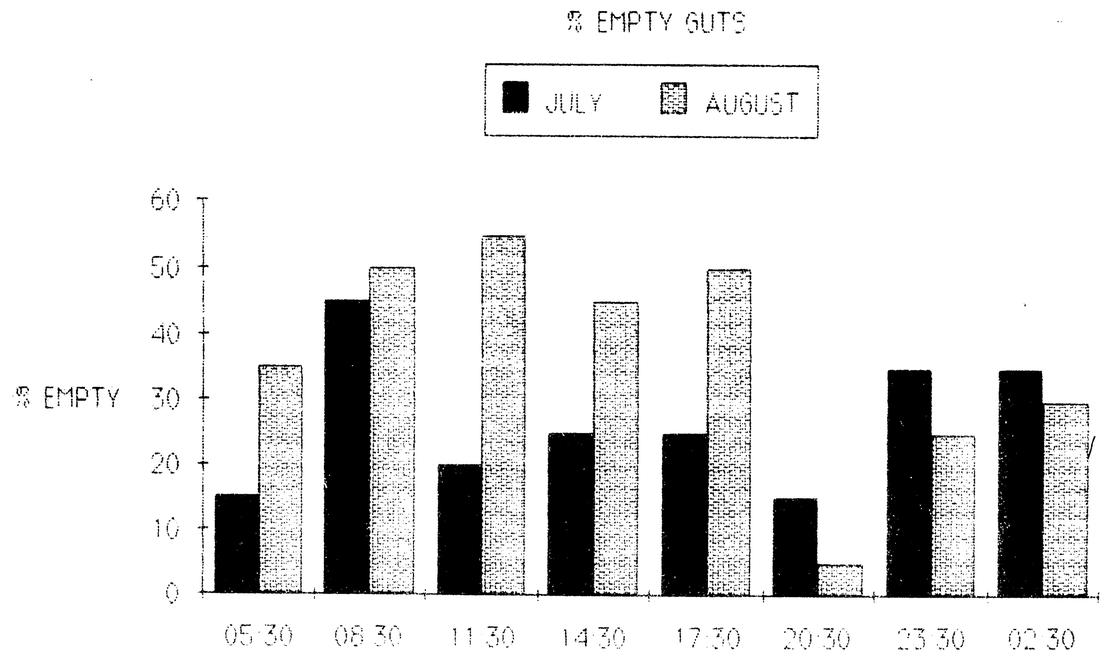


Figure 2 Percentage of 20 guts found empty in each sampling period during July and August.

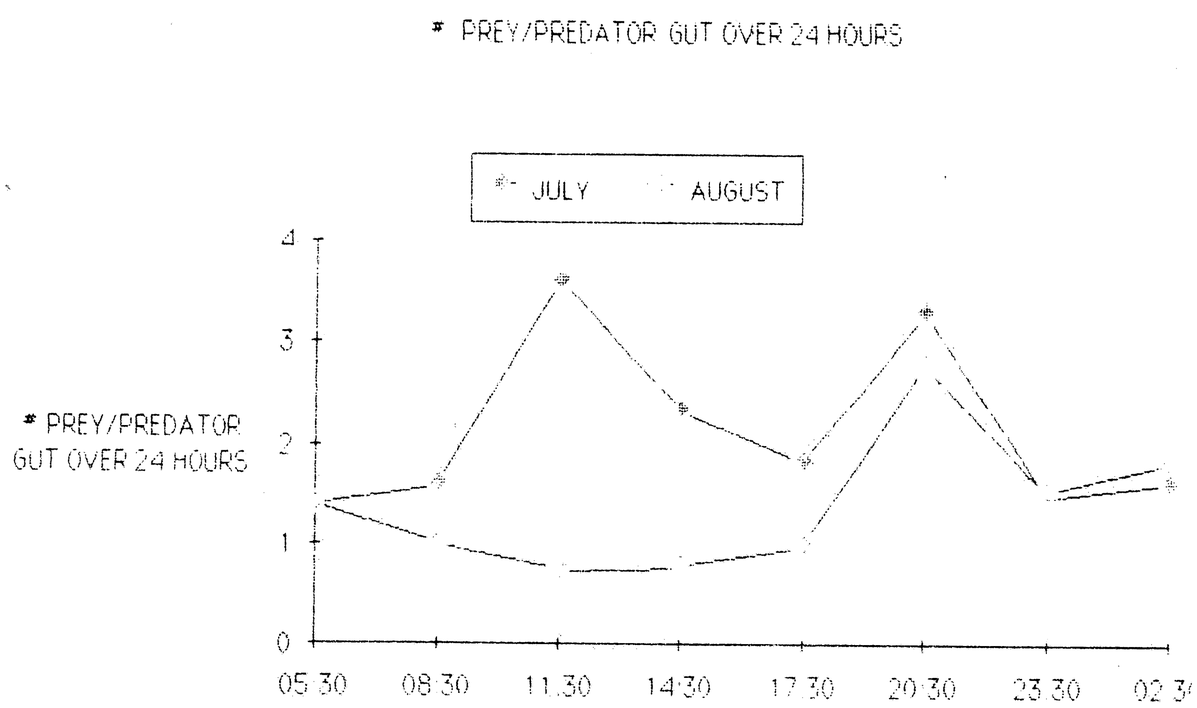


Figure 3 Mean number of prey per predator gut over 24 period hour in July and August

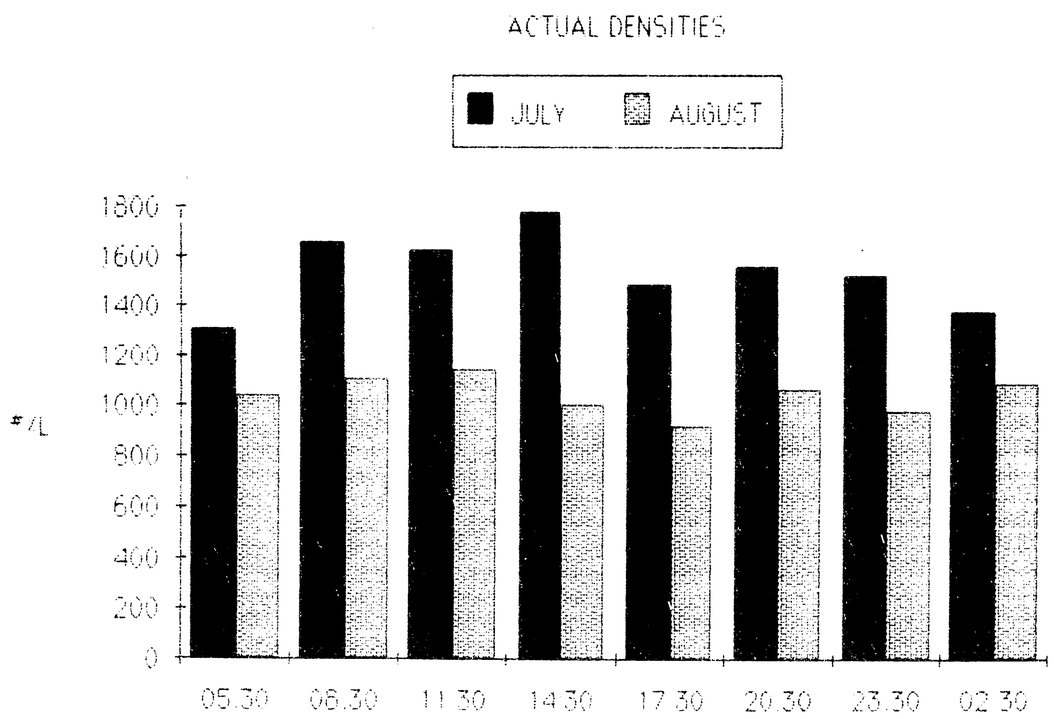


Figure 4. Total density of zooplankton including predators for July and August

The different migrational patterns of predators and prey place the predators in areas of different prey availability both in terms of numbers and vulnerable prey species. If the density of prey species is weighted for predator and prey overlap, the weighted density becomes a better indicator of the number of prey to which a predator is exposed over 24 hours than the absolute number of prey items in the entire water column (Figure 5). The weighted densities are significantly different over the 24-h sampling times in both months ($P=0.0001$) but again there are no peaks in abundance at 1130 and 2030 in July and 2030 in August to account for increased feeding activity.

Since there were significant differences in the numbers of prey available, a regression analysis using data from both months was computed ($n=16$) to determine whether any relationship exists between the number of prey per predator gut and the weighted density of available prey. The regression shows the number of prey per predator gut to be an increasing function of weighted density (Figure 6), but it is not significant ($r^2=0.022$; $P=0.5819$). Ninety-five percent confidence intervals around the mean of Y illustrate that there are three outliers outside this range. These outliers correspond to the peaks in feeding seen during July and August. Removal of the three outliers from the regression result in a significant relationship between prey per predator gut and weighted density (Figure 7; $r^2=0.453$; $P=0.0117$; 95% confidence bands). This suggests that only about 45% of the variation in the ingestion rates can be accounted for by weighted density alone.

Using a normalized ingestion rate (number of prey per predator gut divided by the weighted density) over time it becomes clear that there is an increased rate of ingestion at 1130 and 2030 in July and at 2030 in August that is not accounted for by an increase in

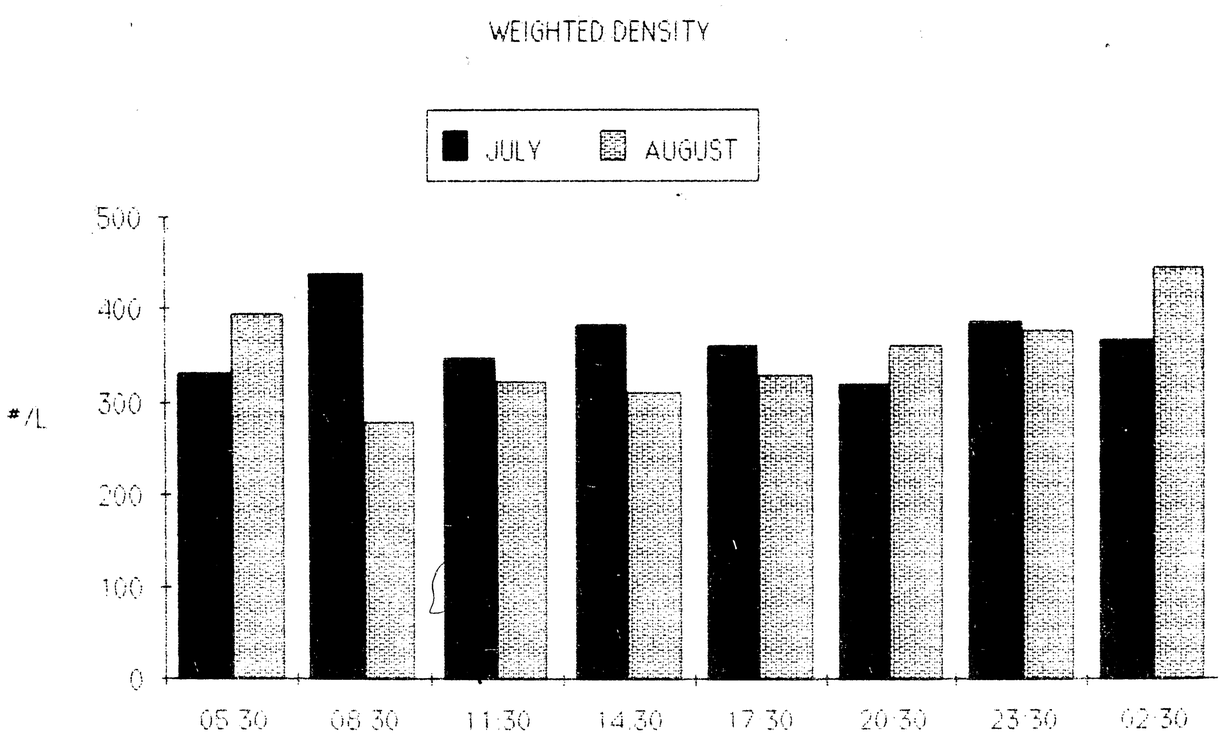


Figure 5 Weighted density of prey in July and August.

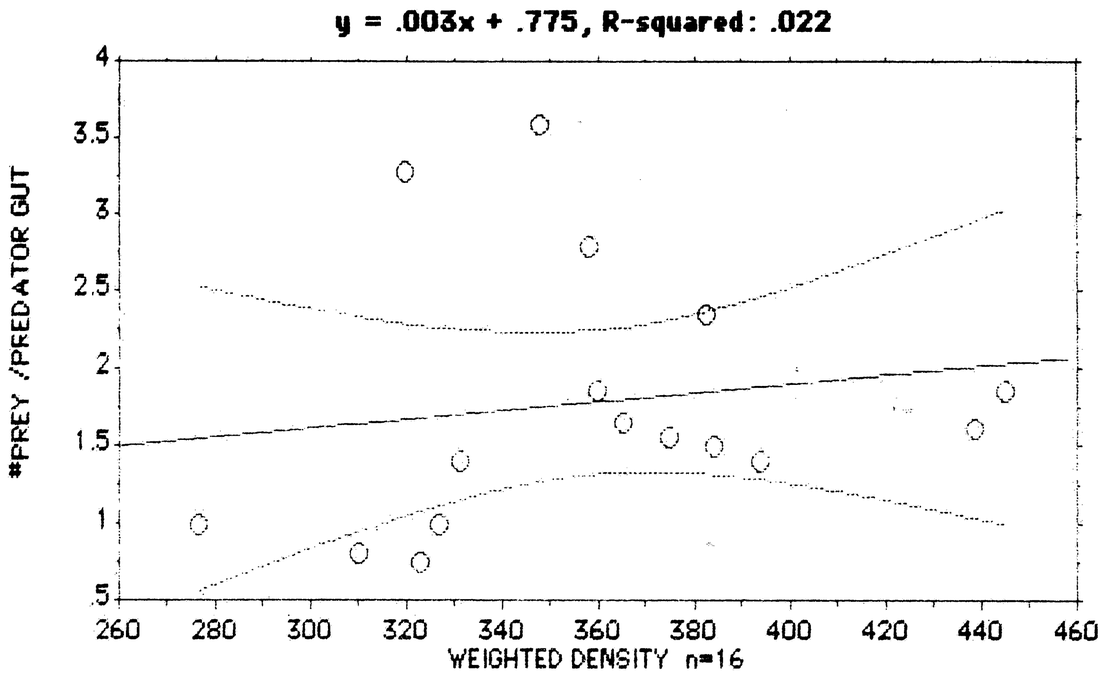


Figure 6. Linear regression of number of prey per predator gut regressed against weighted density using all time periods for July and August.

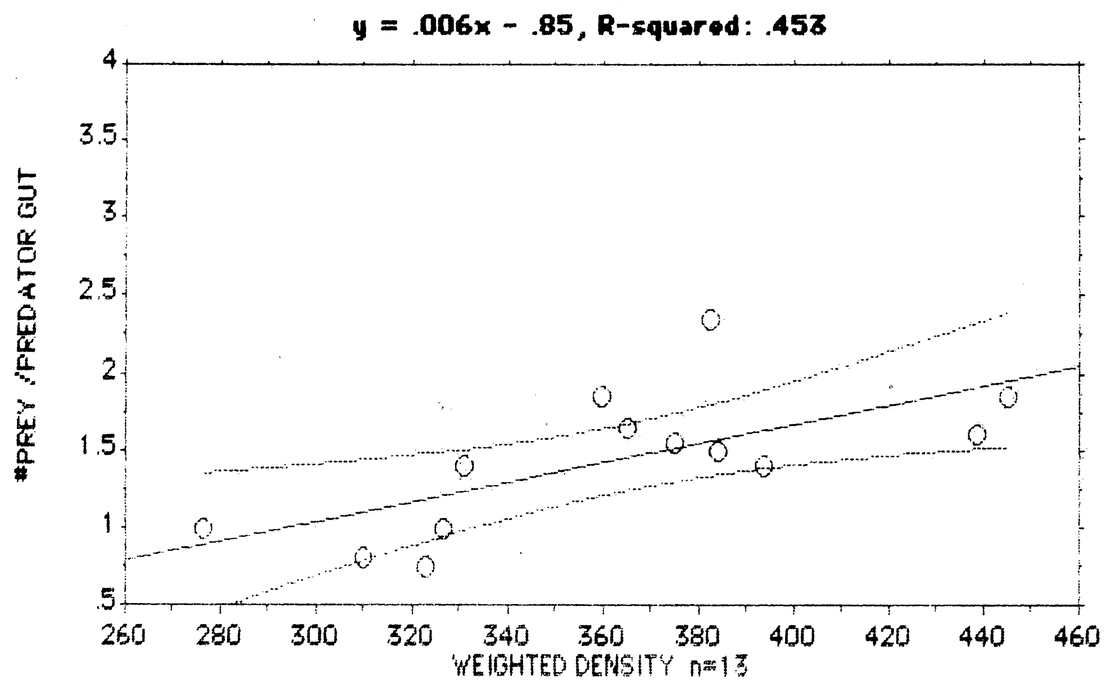


Figure 7. Linear regression of number of prey per predator regressed against weighted density using all time periods except 1130, 2030 in July and 2030 in August.

prey density (Figures 8 and 9).

Using weighted densities alone assume all prey items are equally vulnerable However, clearance rates obtained in the laboratory (using a natural homogeneous zooplankton assemblage) for July and August indicate that the clearance rates (prey vulnerability) differ from one species to another and also between the July and August experiments (Table 1) To account for differences in prey vulnerability the following formula was used to correct for the errors assumed by weighted density alone; this values gives us a more realistic density that accounts for not only overlap but also prey vulnerability

$$\sum_{1}^{m} D_{w1} F_1$$

where m = number of species

D_{w1} = weighted density for species 1

F_1 = clearance rate (prey vulnerability) for species 1

This value should give us some idea of where the highest predation should occur if the predators were feeding in accordance with prey abundance and prey vulnerability Figure 10 illustrates these values over time and suggests that the greatest availability of vulnerable prey occurs at 0830 in July and 0230 in August To view this another way, the deviations from the mean of the weighted density times the clearance rates are graphed

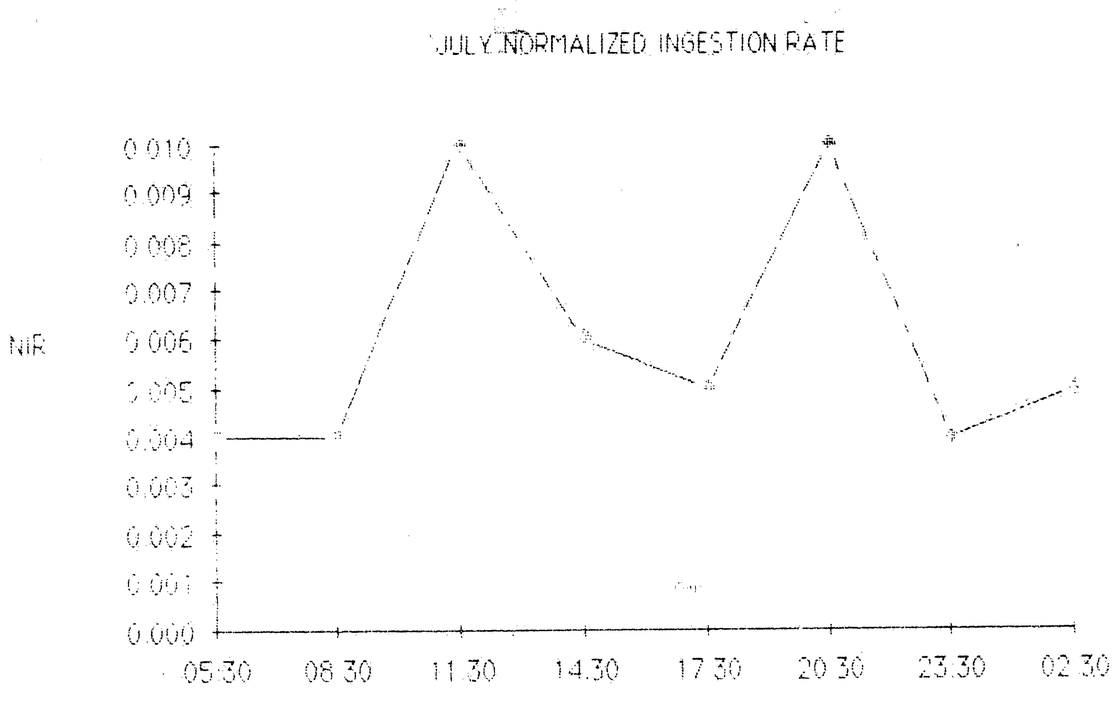


Figure 8 Normalized ingestion rates for July (number of prey per predator divided by the weighted density

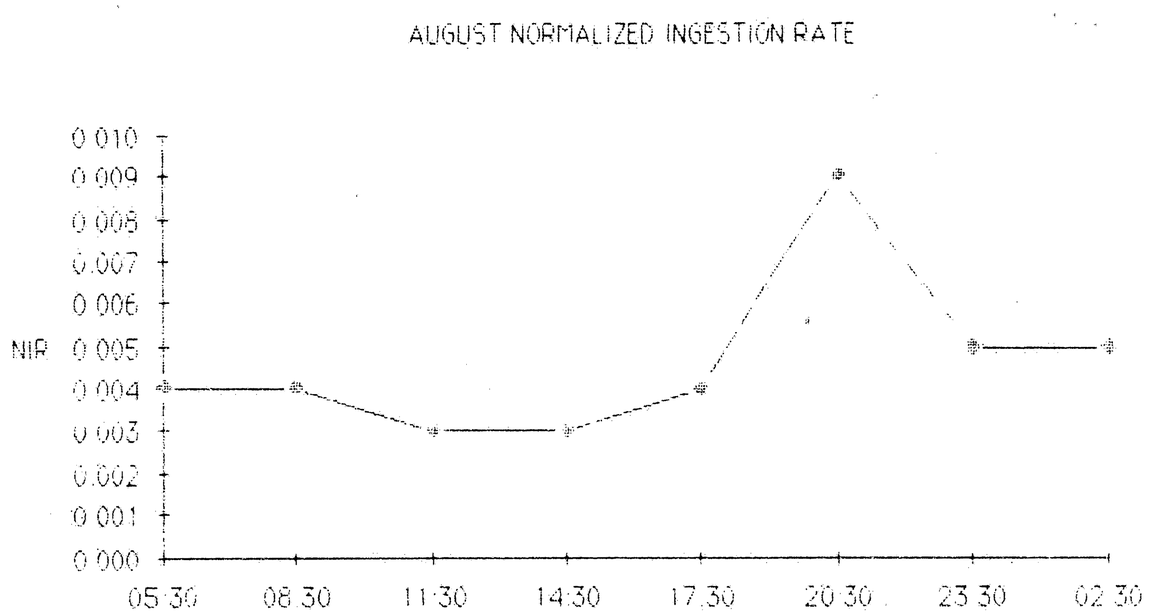


Figure 9 Normalized ingestion rate for August (number of prey per predator divided by the weighted density

CLEARANCE RATE

(ml/pred/day)

	PREY VULNERABILITY		AVERAGE DENSITY	
ROTIFERS	**JULY**	**AUGUST**	**JULY**	**AUGUST**
P. vulgaris	20.1	22.7	150.12	86.64
P. eurvptera	17.5	30.8	59.81	26.43
Asplanchna	65.1	---	38.28	---
Conochilus	19.1	---	352.62	1.43
Gastropus	13.9	7.3	84.43	21.16
Ascomorpha	1.6	---	32.81	3.41
Keratella cochlearis	---	5.1	46	49.30
K. americanus	---	20.8	0	7.62
K. crassa	23.5	10.7	15.3	236.33
CLADOCERANS				
Large Daphnia	2.5	3.7	64.11	18.00
Small Daphnia	37.0	20.2	23.86	4.36
Ceriodaphnia	---	23.0	3.85	12.5
Bosmina	---	15.1	10.10	65.67
COPEPODS				
Tropocyclops, females	12.5	---	12.13	7.59
Tropocyclops, males	9.9	5.2	1.39	7.76
Copepodites	4.9	19.4	33.07	66.15
Nauplii	11.9	12.0	238.8	205.5

Table 1. Clearance rates (prey vulnerability) and densities for all species in July and August

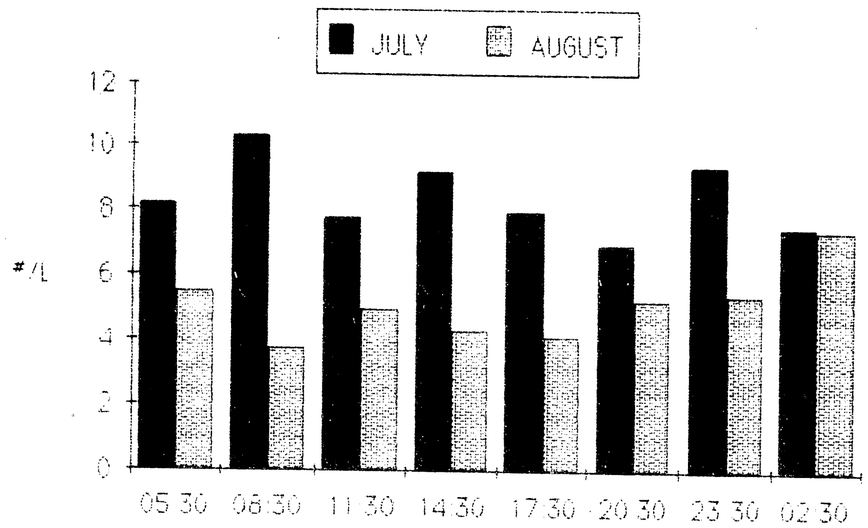


Figure 10 Weighted density multiplied by prey vulnerability (clearance rates). This value considers both predator-prey overlap and prey vulnerability

(Figure11) and it shows that the times of greatest abundance are not coincident with the peaks of feeding activity at 1130 and 2030 in July and 2030 in August Although there is a slight elevation in the deviations from the mean at 2030 in August it is not as great as the 0230 sample.

When number of prey per predator gut are regressed against weighted density times the clearance rates the r^2 value is only 0 136, which is not significant (P=0 1602; 95% confidence bands around the mean of Y. Figure 12) However, when the three peaks of feeding are removed and the regression repeated, the r^2 value is substantially increased to 0.543 and this is significant at the P=0.004 level (Figure 13; 95% confidence bands around the mean of Y)

Vanderploeg and Scavia's E* (1979) selectivity index was used to determine the selectivity of prey items during the July and August 24 -h samplings (with modifications discussed in the methods). The E* values were grouped into three categories rotifers, cladocerans, or copepods (individual E* values were also computed for the rotifers) E* values were calculated for each of the eight sampling periods (Figures 14 and 15) and then one composite E* value was computed for each of the three groups in July and August (Figure 16). The patterns of selectivity for rotifers, cladocerans, and copepods changed significantly (P= 0 0001) over the eight time periods in both months examined but the general pattern of selection was for rotifers, then cladocerans, and finally copepods

Due to the change in overlap between predator and prey the copepods may be selecting for different prey items based on what's available at different times. In this study I have adjusted for the differences in predator and prey overlap in calculating the E* values In the 24 hour study in July the copepods selected against cladocerans from 1430 until

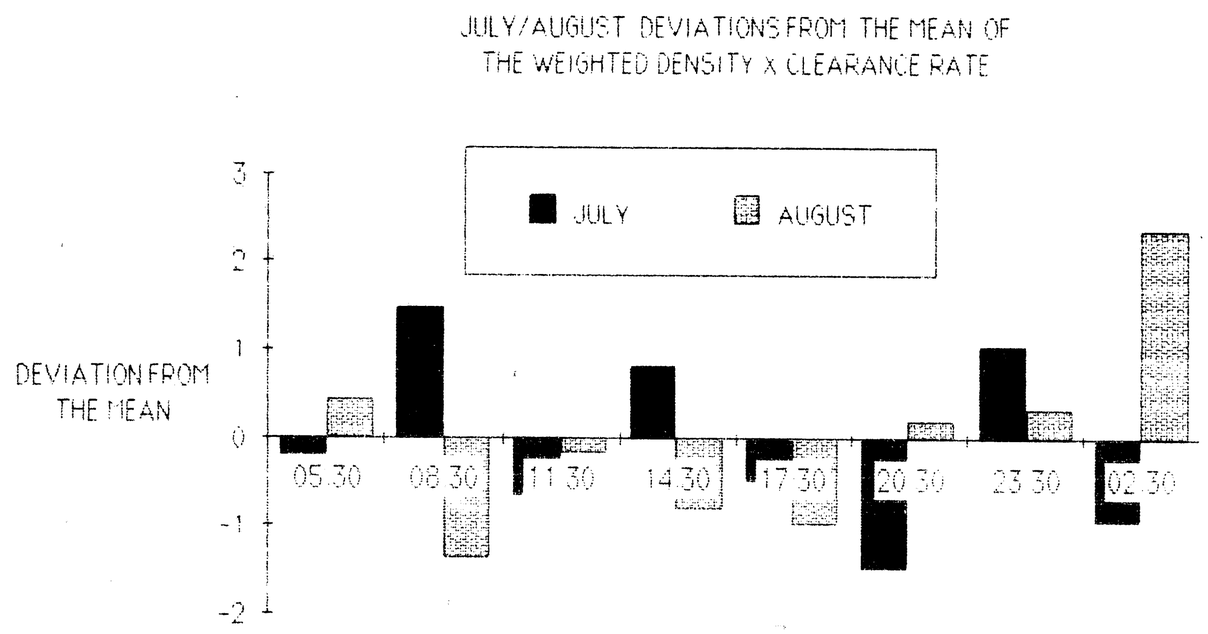


Figure 11. July and August deviations from the mean of the weighted densities times the clearance rates

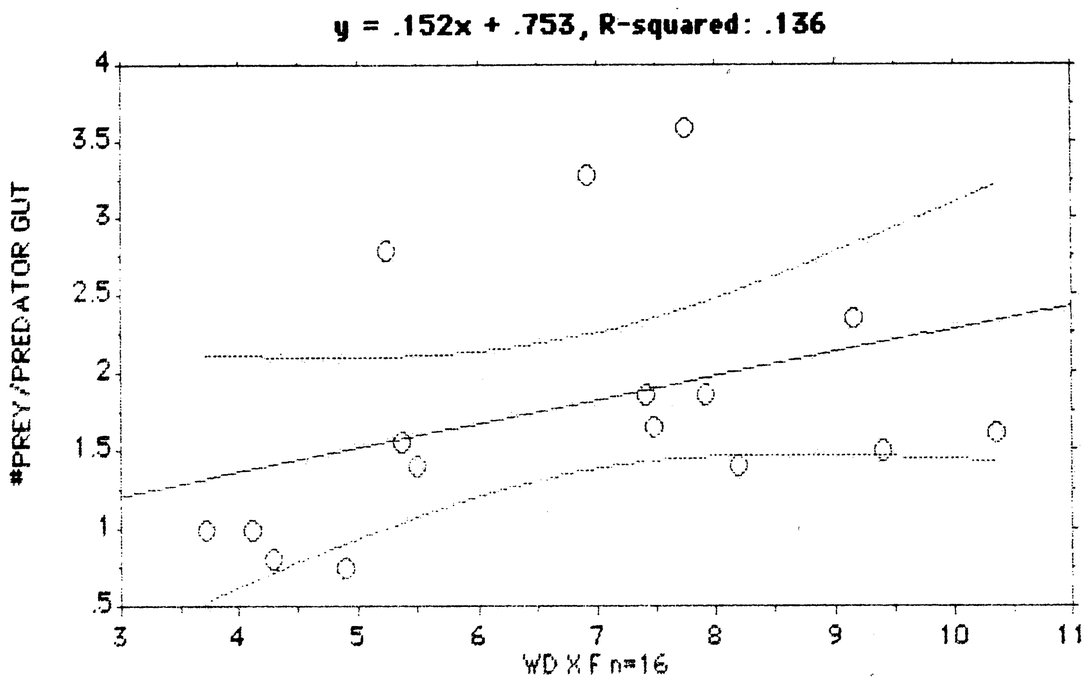


Figure 12. Linear regression of number of prey per predator regressed against weighted density (WD) times prey vulnerability (F) for July and August.

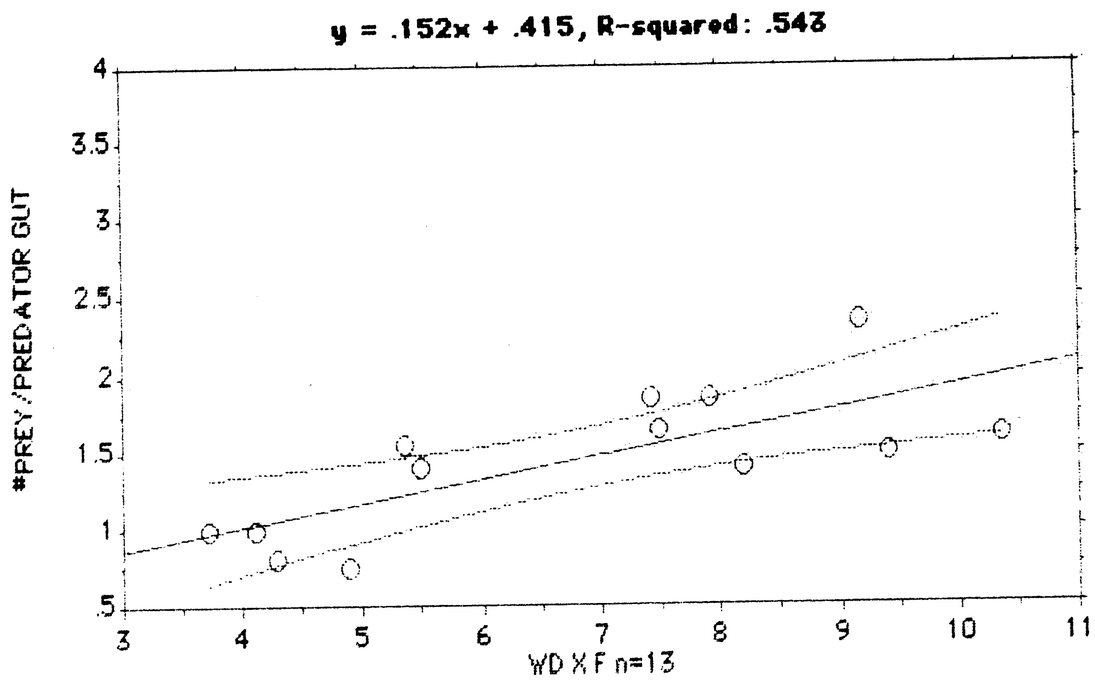


Figure 13. Linear regression of the number of prey per predator regressed against weighted density (WD) times prey vulnerability (F) for July and August minus July 1130,2030 and August 2030.

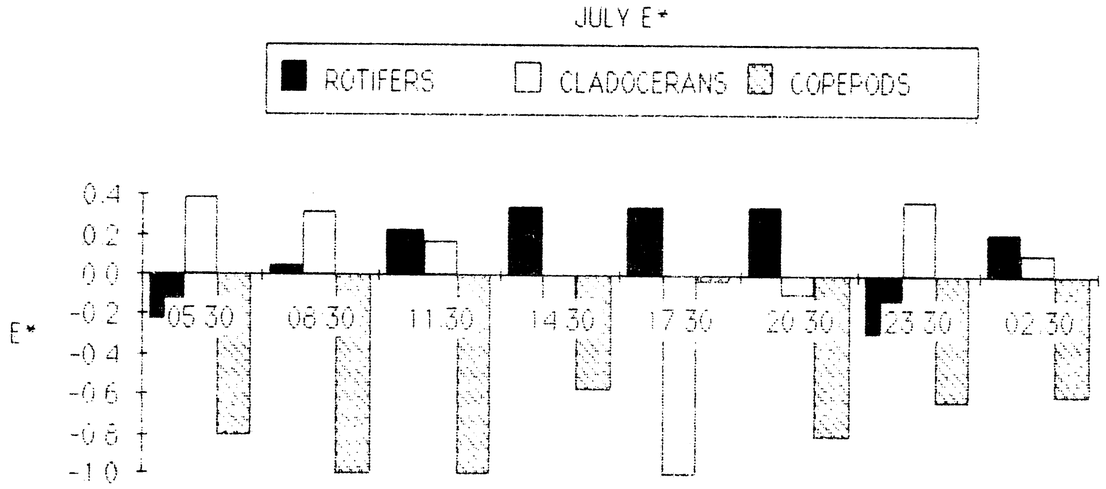


Figure 14 Selectivity index (E*) for rotifers, cladocerans, and copepods over 24 hours on 9 July, 1986. Positive values indicate preference, 0 values indicate random feeding, and negative values indicate avoidance.

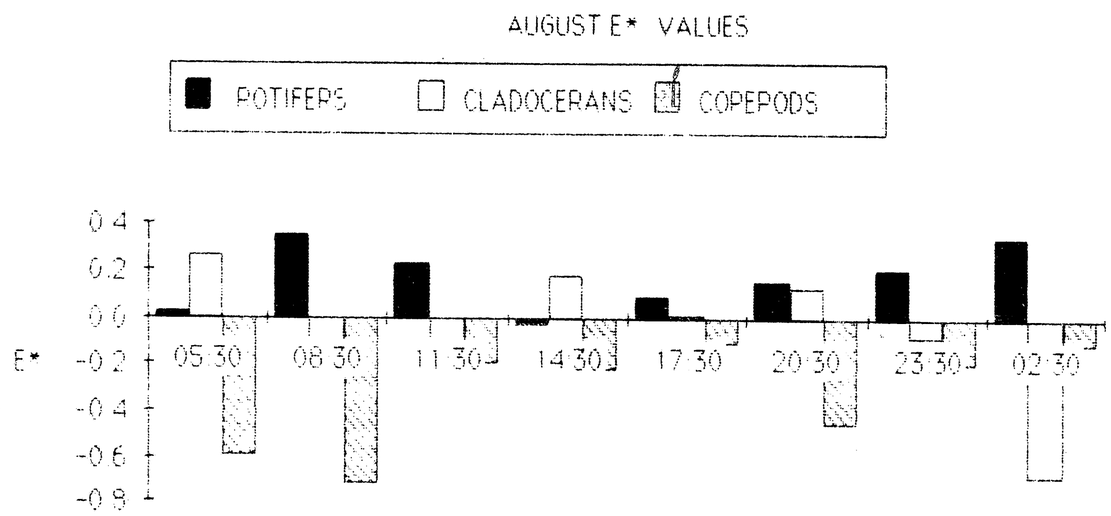


Figure 15. Selectivity index (E*) for rotifers, cladocerans, and copepods over 24 hours on 9 July, 1986. Positive values indicate preference, 0 values indicate random feeding and negative values indicate avoidance

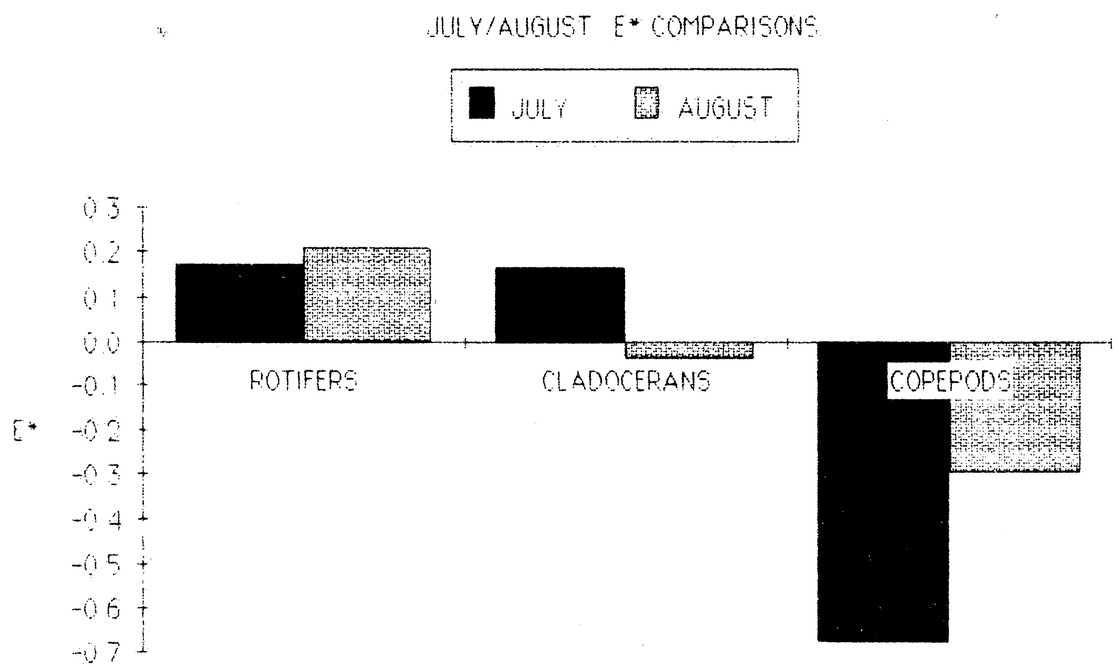


Figure 16 Selectivity index (E*) comparisons for July and August

2330 and rotifers were selected against at 0530 and 2330 (Figure 14). In August, rotifers were almost never selected against (but slight negative values are shown for 1430) and the selection for cladocerans show a mixed positive and negative selection throughout the day (Figure 15). Copepods were always avoided (Figures 14, 15, 16). However, since the system is so complex the important point here is that there is a difference in overall selectivity

In the comparison between techniques for estimating ingestion rates, gut content analysis and enclosure experiments gave similar results for both techniques when actual densities were used and compared to a 3h gut passage time (Table 2) However, when weighted densities were used, similar results were obtained with a 5h gut passage time (Table 3)

ACTUAL DENSITIES

	INGESTION RATES ENCLOSURE EXPERIMENTS	INGESTION RATES GUT ANALYSIS (gut passage)		
JULY				
H_0: Both techniques give similar results		3 h	4 h	5 h
Asplanchna	2 490	2.248	1.686	1.349
Polyarthra	21 99	8.200	6.150	4.920
Conochilus	6 735	2 704	2 028	1 622
P. eurvptera	1.047	1.504	1.128	0.9024
Gastropus	1 174	0 4000	03000	0 2400
Ascomorpha	0 0525	0 1520	0 1140	0 0910
Cladocerans	1.043	1.552	1 164	0.9310
Copepods	3 169	0.5040	0 3780	0 3020
		$\Sigma+=28$	$\Sigma+=30$	$\Sigma+=35$
		$\Sigma-=8$	$\Sigma-=6$	$\Sigma-=1$
		$T_s=8$	$T_s=6$	$T_1=1$
		NS	NS	S(0 0156)
AUGUST				
Polyarthra	8 687	5 648	4 236	3 389
P. eurvptera	0 814	1.000	0 7500	0 6000
Keratella	2 939	1 400	1 050	0 8400
Gastropus	0 1540	0 0480	0 0360	0 0290
Cladocerans	1 433	1.000	0.7500	0.6000
Copepods	3 790	1.552	1 164	0 9310
		$\Sigma+=19$	$\Sigma+=21$	$\Sigma+=21$
		$\Sigma-=2$	$\Sigma-=0$	$\Sigma-=0$
		$T_s=2$	$T_s=0$	$T_s=0$
		NS	S(0 0312)	S(0 0132)

Table 2. Estimated ingestion rates (number of prey per predator) for July and August. Values used for the Wilcoxon Signed-Rank test include ingestion rates from actual densities in the water column times the clearance rates and ingestion rate estimates using three gut passage times. Results indicate that 3h gut passage time gives similar results to enclosure experiments (NS=not significant at 0.05, S=significant).

WEIGHTED DENSITIES

	INGESTION RATES ENCLOSURE EXPERIMENTS **JULY** H_0 Both techniques give similar results	**INGESTION RATES** GUT ANALYSIS (gut passage) 3 h	4 h	5 h
Asplanchna	0.4520	2.248	1.686	1.349
Polyarthra	4.698	8.200	6.150	4.920
Conochilus	1.670	2.704	2.026	1.622
P. eurvptera	0.1080	1.504	1.128	0.9024
Gastropus	0.3470	0.4000	0.3000	0.2400
Ascomorpha	0.0160	0.1520	0.1140	0.0910
Cladocerans	0.2890	1.552	1.164	0.9310
Copepods	0.6690	0.5040	0.3780	0.3020
		$\Sigma+=3$	$\Sigma+=4$	$\Sigma+=9$
		$\Sigma-=33$	$\Sigma-=32$	$\Sigma-=27$
		$T_s=3$	$T_s=4$	$T_s=9$
		S(0.0390)	NS	NS
AUGUST				
Polyarthra	1.996	5.648	4.236	3.389
P. eurvptera	0.235	1.000	0.7500	0.6000
Keratella	1.025	1.400	1.050	0.8400
Gastropus	0.0340	0.0480	0.0360	0.0290
Cladocerans	0.5190	1.000	0.7500	0.6000
Copepods	1.117	1.552	1.164	0.9310
		$\Sigma+=0$	$\Sigma+=0$	$\Sigma+=8$
		$\Sigma-=21$	$\Sigma-=21$	$\Sigma-=13$
		$T_s=0$	$T_s=0$	$T_s=8$
		S(0.0312)	S(0.0312)	NS

Table 3 Estimated ingestion rates (number of prey per predator) for July and August. Values used for the Wilcoxon Signed-Rank test include ingestion rates from weighted densities in the water column and ingestion rates estimates using three gut passage times. Statistics indicate that a 5h gut passage time gives results similar to enclosure experiments. (NS=not significant at 0.05, S=significant)

DISCUSSION

Daily changes in the feeding activity of Mesocyclops edax were demonstrated on 9 July at 1130 and 2030 and 5 August at 2030 in Hellertown Reservoir. These changes in the feeding activity could be caused by several factors: changes in the prey density of the water column, changes in the overlap between predator and prey, or changes in the copepod's daily rhythm. In the last case, the periodicity may be a result of recurrent environmental stimuli (such as light or darkness) or due to internal oscillations of the circadian type as entrained by exogenous stimuli (zeitgeber effects).

Ingestion rates of Mesocyclops edax are density dependent (Confer, 1971). In the present study, the observed increases in feeding activity were not soley dependent on prey density as expected. When the three times of peak ingestion were removed from the regression analysis the regressions on ingestion rates versus weighted densities do show an increase in the ingestion rate with increasing weighted densities (r^2=0.453, P=0.0117). This implies that while ingestion rates generally are density dependent, increases in ingestion rates at certain times of the day cannot be accounted for by density alone. When prey vulnerability was considered along with predator-prey overlap, prey availability still did not account for the increases in feeding (Figures 12 and 13).

Daily feeding changes have been described for some marine zooplankton and these studies have attributed the changes to migrations into and out of food rich layers (Calanus, Gauld, 1951) or to differences in developmental stages (Calanus, Petipa, 1964), or to changes in the light dark cycle. Bainbridge (1958) reported daily changes in gut contents of Evadne, a marine cladoceran, with maximal feeding rates occurring during the daylight hours for this visual predator.

Studies concerned with diel patterns of feeding in freshwater communities have focused mainly on the cladoceran Daphnia. Haney & Hall (1975) found there were daily changes in filtering rates of Daphnia during diel vertical migrations. They recorded low filtering rates during the day when the Daphnia were in the deeper waters and an increase in filtering rates as Daphnia ascended the water column in the evening. This increase in filtering rate was followed by a decrease at midnight with another peak occurring in the morning before the organism descended into the deeper waters where they maintained a low filtering rate until the cycle began again at dusk. However, in this study Diaptomus were also monitored and no such change in filtering rate pattern was observed. Starkweather (1983) also working with Daphnia agreed with Haney & Hall in that the maximum filtering rates were greatest during the dark phase of the LD cycle. Duval & Geen (1976) found significant bimodal feeding activity changes for mixed freshwater species groups with maxima near dawn and dusk, the differences in feeding were 6.6 times higher at dawn and dusk than at the midday lows. The present study agrees in part with the above studies in that there was a peak in feeding that occurred at dusk (2030) in both months. The increase in feeding observed in this study was a six fold increase in ingestion between the highs at dusk and the lows during the day (Figures 8 and 9). However, the peak in feeding at 1130 is difficult to resolve. It must also be noted that Daphnia is an herbivore and may exhibit very different patterns of feeding based on dietary differences. M. edax, a carnivore, might not be expected to have evolved the same feeding patterns.

Many daily rhythms are associated with the light- dark cycle. Vertical migration in zooplankton is one of these. Two of the three peaks in feeding activity occurred at 20:30-

near the times of sunset which were 20:35 in July and 20:13 in August. This suggests that the effects of environmental stimuli such as the light -dark cycle need to be further investigated. This may be especially true for the 1130 increase in feeding. Tables 4 and 5, show the light readings in the water column on the two sampling dates. Since the light reading for July 1130 was not available the light readings from the week after at 1130 (Table 6) were used to construct a graph (Figure 17) demonstrating the mean light in the water column at each time period (we did have a record of the weather conditions). July 9 was a cloudy day and the light levels were especially low. The low light levels in the water column over the entire day may have acted as a stimulus which may have caused the increase in feeding. However, this does not explain why there was an increase in feeding at 1130 and not at other times during the day, although hunger level may have been a factor. The low light levels in the water column in July were the only differences between July and August that might have made a difference in the feeding. This aspect will have to be further investigated to see what effect this may have on feeding behavior.

In the second part of this study the selective feeding of M. edax over 24 hours and also between two sampling times in July and August was examined. The selective feeding of Mesocyclops has been demonstrated by several authors (Confer, 1971, Brandl & Fernando, 1978, 1986; Williamson 1980, Williamson & Magnien, 1982). While selection has been demonstrated, the variability in the selectivity of Mesocyclops as the zooplankton assemblage changes over 24 hours has not been fully examined. From the evidence reported here the selectivity index demonstrated that rotifers were generally the prey of choice with cladocerans being chosen some of the times and copepods never receiving positive selection. It has also been shown that the positive selection for

HELLERTOWN RESERVOIR
1986

LIGHT (FOOT CANDLES)
JULY

	05:30	08:30	11:30	14:30	17:30	20:30
ABOVE	58	500	-	660	500	410
0 meters	37	260	-	380	290	9
1	26	170	-	280	190	6.9
2	21	140	-	220	140	4.9
3	15	87	-	150	71	3.3
4	9.3	54	-	88	46	2.3
5	6.8	42	-	65	34	.74
6	5.3	31	-	49	26	.50
7	4.2	25	-	38	7.4	.36
8	3.5	18	-	27	6.4	.16
9	2.3	9.8	-	18	4.5	.3
10	.76	2.5	-	1.2	.58	0
AVERAGE (W/O ABOVE)	11.9	76.3	-	118.1	74.17	2.6

Table 4. Light readings in foot candles for July 9, 1986

HELLERTOWN RESERVOIR
1986

LIGHT (FOOT CANDLES)
AUGUST

	05:30	08:30	11:30	14:30	17:30	20:30
ABOVE	14	500	5000	-	7000	36
0 meters	8	720	5000	2700	5000	16
1	6	420	1500	1700	2000	06
2	4	210	1300	1200	1400	.05
3	3	120	730	600	770	.03
4	16	52	330	270	350	02
5	.12	24	140	110	160	0
6	11	15	78	57	77	0
7	11	10	56	37	53	0
8	10	57	33	25	35	0
9	10	28	12	6.1	95	0
10	.09	13	.25	.12	.12	0
AVERAGE (W/O ABOVE)	2.0	143.6	834.5	609.6	881.6	.03

Table 5. Light readings in foot candles for August 5, 1986

HELLERTOWN RESERVOIR
1986

LIGHT (FOOT CANDLES)

	JULY 03, 1986 (SUNNY)	JULY 16,1986 (OVERCAST)
ABOVE	-	870
0 meters	1700	540
1	1500	540
2	740	260
3	500	170
4	360	90
5	340	48
6	210	30
7	170	20
8	130	15
9	76	8.8
10	2	1.5
AVERAGE (W/O ABOVE)	520.7	108.1

Table 6. Light readings in foot candles for July 3, and July 16, 1986.

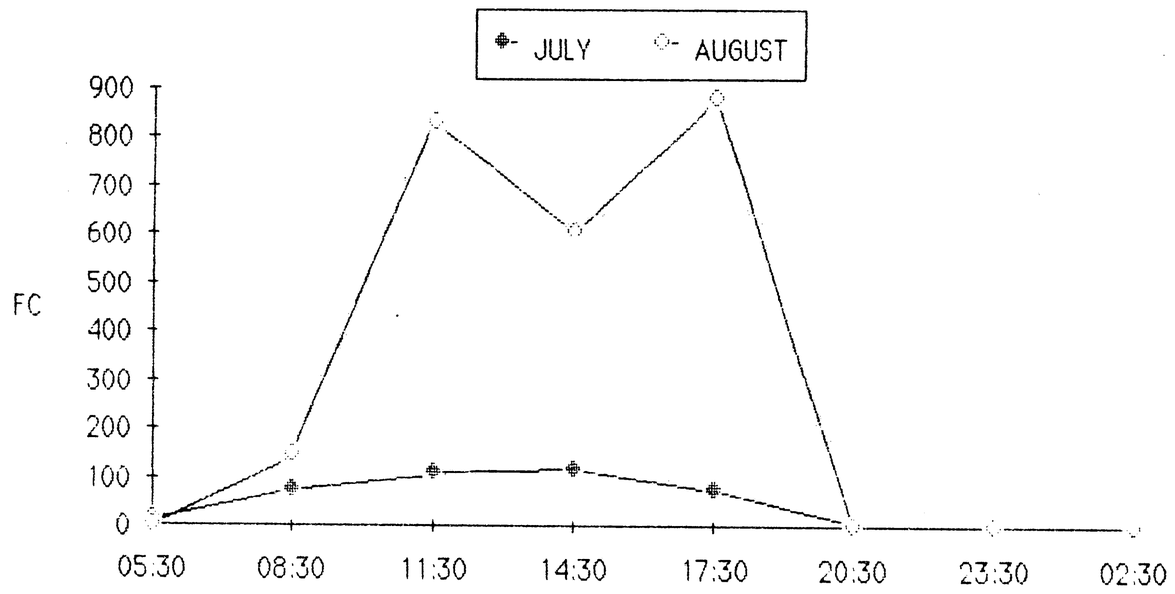


Figure 17. Average foot candles found throughout the water column 9 July and 5 August. 11:30 reading for July was taken from 16 July.

cladocerans changes between July and August.

The change in the selectivity for cladocerans between July and August can be attributed to the change in species composition and also prey vulnerability during the two sampling dates. The change in species composition shows that there was a change in the cladoceran community from one dominated by large and small Daphnia in July (87.97/L in July; 22.36/ L in August) to one dominated by Bosmina and Ceriodaphnia in August (13.95/L in July; 78.17/L /L in August)(Table 1). These changes in species composition reflect a threefold decline in density for large Daphnia and a sixfold decline in density for small Daphnia while the changes in density for Ceriodaphnia reflect a threefold increase and for Bosmina, a sixfold increase. The clearance rates or prey vulnerability (PV) from the laboratory experiments show that large Daphnia's PV changes very little between months (2.5 in July to 3.7 in August) and that small Daphnia's PV changes considerably (37 in July to 20.2 in August) while Ceriodaphnia (.23) and Bosmina (15.1) have somewhat intermediate clearance rates in August (no clearance rates were available for July due to low density). The lower clearance rates for Ceriodaphnia and Bosmina and the decline in the Daphnia species and PV could account for the shift in selection of cladocerans from positive to negative between July and August. The twofold increase in copepodites in August (33.07/L in July; 66.15/L in August) and the almost fourfold increase in PV (4.9 in July; 19.4 in August) may also have had an impact on the increased selection for copepods found in the August guts (Figure 16).

Figure 18 illustrates the proportion (r) of each group of prey making up the diet in July and August. Rotifers are the most abundant prey choice for both months, while cladocerans are an equally abundant part in both months. The increase in abundance of

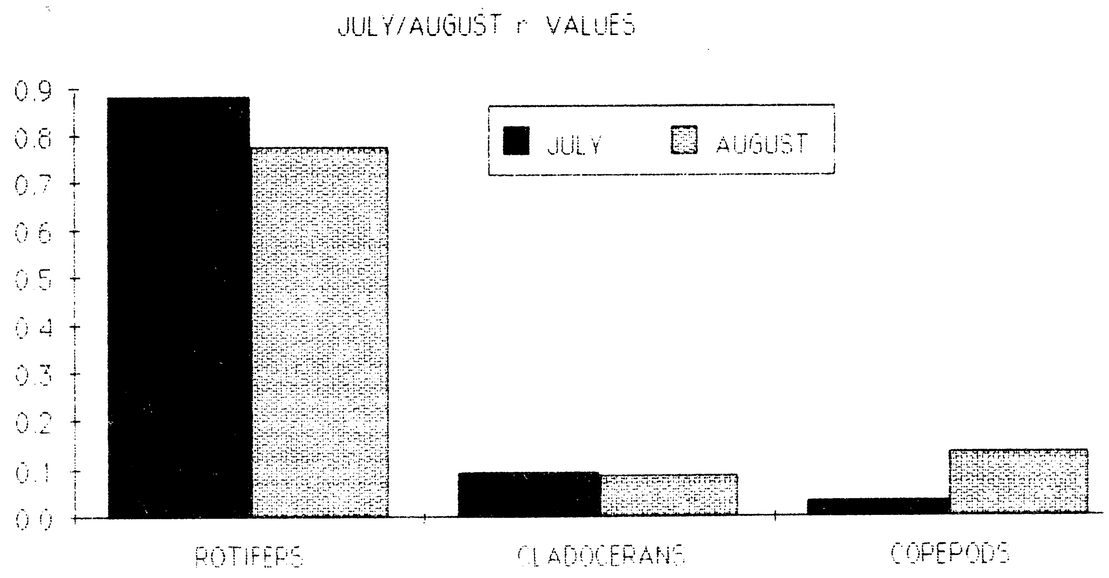


Figure 18. Comparison of r values for July and August. These values represent the proportion of the prey type in the diet

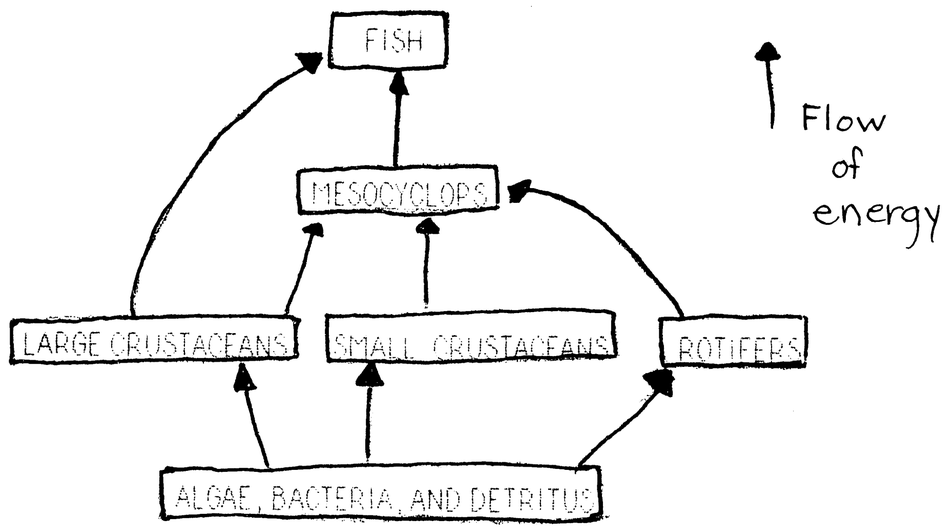
copepods in the diet from July to August is probably due to the increase in the density of copepods in the water column at this time (Table 1)

Biomass was not used to determine its effect on the number of prey eaten. Other laboratory investigators (Confer, 1971, Williamson, 1984) have indicated that copepods feeding on cladocerans and copepods do not always eat whole organisms. Often only parts of the animal are eaten and other times only the soft parts are scraped out of the animals. Since gut contents are only as good as the amount of remaining prey left in the gut, biomass comparison would not be any better than the gut content analysis and therefore was not used.

The positive selection for rotifers in this study agrees with the studies of Brandl & Fernando (1978, 1979) and Williamson (1984). Williamson (1984) reported that naupli and copepodite stages were of sporadic importance and that Bosmina and Daphnia were eaten depending on the hunger level of the copepods. However, Confer (1971) found that Diaptomus floridanus copepodites were chosen over cladocerans in experiments that were run for two to five days. Since there were no calanoid copepods in Hellertown Reservoir, this may have accounted for the greater selectivity for cladocerans over copepods in this study.

The abundance of the rotifers in the diet and the high selectivity for the rotifers indicates that the copepods will have a dramatic impact on the rotifer community. This impact can manifest itself in several ways. the impact of predation can affect the numbers of prey in the system, the size structure of the community, the succession of other plankton, and can also be responsible for altering the morphology or behavioral aspects of the prey defenses of the rotifers most heavily preyed upon (Williamson et al. in review)

By consuming the rotifers in the system, Mesocyclops plays an impotant role in the trophic dynamics of the aquatic system. In resent years research has focused on both the indirect and direct effects of predation on the trophic interactions of a community (Kerfoot & Sih, 1987). Miller & Kerfoot (1987) have defined indirect effects of a species as an effect that modifies the direct effect of one species on another. Mesocyclops edax is an ecologically and evolutionaly important organism that plays a critical role in the trophic dynamics of aquatic ecosystems. Ecologically its importance in the flow of energy through the system can be best shown by a simple food web



Visual predators such as Lepomis macrochirus and Micropterus salmoides are two planktivores found in Hellertown Reservoir which prey upon Mesocyclops and large crustaceans such as Daphnia. Daphnia are grazers which feed on algae, bacteria, and detritus, the smaller crustaceans and rotifers are also grazers that feed on algae, bacteria, and detritus. Mesocyclops, an invertebrate predator, feeds on different trophic levels depending on its life stage. The nauplii feed on algae, bacteria, and detritus, but as

they reach the late copepodite stages they becomes increasingly carnivorous until as adults, they are almost entirely carnivorous (Wyngaard & Chinnappa, 1982) As you follow the flow of energy up the system it becomes clear that Mesocyclops is instrumental in utilizing the energy from the rotifers and small crustaceans and carrying it up the system.

Indirect effects of predation need to be considered. If a predator is selectively preying on a particular organism or group of organisms such as the rotifers, algal species and therefore otherplankton will be indirectly affected by this predation. For instance, with fewer rotifers, more algae may be available to the other herbivores and depending on the competitive ability of these herbivores, the size structure of this community could be shifted upward or downward. If the larger crustaceans are better competitors, then there will be a decrease in the number of small crustaceans and an increase in the number of large crustaceans and the size structure would be shifted upward. If the smaller crustaceans are better competitors, then the large crustaceans will decrease in density, the small crustaceans will increase in density and the size structure would be shifted downward. These shifts in the size structure will have an impact on the upper trophic levels as well. With an increase in large crustraceans, an increase in fish predation would result. On the other hand with an increase in the small crustaceans, the invertebrate predators would increase

The final portion of this study was to determine how well ingestion rate estimates from 24 hour laboratory enclosure studies using natural assemblages of zooplankton compare to gut content analysts of preserved copepods from 24 hour sampling that estimate ingestion rates. Results (Table 2 and 3) indicate that the two methods are statistically equivalent

if actual densities and a 3h gut passage time are used or if weighted densities and a 5h gut passage time are used This portion of the study suggests that by performing laboratory experiments over 24 hours the differences in diel periodicity and the changes in selectivity that occur over 24 hours should be less of a problem in performing laboratory experiments than estimate predation rates Future investigators should use natural prey densities and natural prey assemblages in order to determine true selectivity of the organism and its potential impact on the selected organisms in the community

Daily rhythms in freshwater zooplankton have received very little attention and it is an area that needs to be explored more fully if we are to perform meaningful experiments in the future

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APPENDIX

Weighted Density = average density of prey species i in the water column times the overlap value of prey species i. This value represents the density of prey species i weighted for overlap

VITA

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